

**Thesis/
Reports
Nature
Conservancy**

**The Effects of Fire on Silene
Spalding II at Dancing
Prairie Preserve**

COOP AGREEMENT
NATURE
CONSERVANCY

FINAL REPORT FOR RESEARCH AGREEMENT

#INT-93781-CCSA

"Effects of Fire on *Silene Spaldingii* at
Dancing Prairie Reserve"

NATURE CONSERVANCY, The

FS Contact: Dr. Stephen F. Arno

CoOp Contact: Mr. Bernie Hall

THE EFFECTS OF FIRE ON *Silene spaldingii*

AT DANCING PRAIRIE PRESERVE

Draft Final Report

Peter Lesica
The Nature Conservancy
32 South Ewing
Helena, Montana 59601

Supported in part by
USDA Forest Service
Intermountain Research Station
Agreement INT-93781-CCSA

January 1997

Effects of Fire on the Demography
of the Herbaceous Geophytic Herb, Silene spaldingii

Abstract

Understanding the effects of disturbances such as fire on plant demography helps elucidate the mechanisms causing changes in population size and community composition. I studied the effects of spring and fall fire on Silene spaldingii, an endangered perennial herb of grasslands in northwest Montana. Individual S. spaldingii plants were mapped, and size and flowering were recorded for one year prior and five years subsequent to the burn treatments. Enhanced recruitment and an increase in population size were the principal effects of fire on S. spaldingii. Fall burn plots had lower recruitment than spring burn plots. The number of flowers per reproductive plant was greater in burn plots, but the proportion of reproductive plants was greater in control plots than for the fall burn. These effects were apparent for 2-3 years following the treatments. Fire had no detectable effect on the survival of adults or recruits of S. spaldingii. Silene spaldingii exhibits prolonged dormancy in which plants do not produce above-ground vegetation for one to several consecutive years. The proportion of dormant plants was lower in 1993 compared to 1994 for treatments and control, but summer dormancy was higher in burn plots in 1993 but higher in controls in 1994. Results suggest that fire has a positive effect on the population dynamics of S. spaldingii by removing litter and creating safe sites for recruitment. Prescribed fire should be an important tool for managing populations of this rare plant.

Introduction

Disturbance is an important force structuring many plant communities, and is thought to be responsible for maintaining species diversity in numerous biological systems (Huston 1994, Pickett and White 1985, Sousa 1984). Disturbances often remove dominant competitors, temporarily providing adequate water, nutrients and light for establishment (Grime 1979, Grubb 1977). Many plant species are adapted to regular disturbance regimes and may even require disturbances such as fire, windthrow, or grazing to persist (Denslow 1980, Pickett 1980, Sousa 1984, Watt 1981).

Fire is an important disturbance in many grassland, shrubland and forest ecosystems in North America and throughout the world (Kozloski and Ahlgren 1974), and its effects vary among these systems. Fire can remove much or all above-ground biomass, increasing light penetration to the soil surface and often raising surface temperatures (Hulbert 1969, 1988; Peet et al. 1975). Combustion of live and dead fuels or removal of litter layers may result in enhanced nutrient availability (Brewer 1995, Dudley and Lajtha 1993, Knapp and Seastedt 1986, Raison 1979). Fire may also stimulate germination of species adapted to recently fire-disturbed sites (Daubenmire 1968, Glenn-Lewin et al. 1990). The effects of fire vary among plant species, some responding positively and others negatively (Daubenmire 1968, Howe 1995, Vogl 1974).

Numerous plant responses to fire in grasslands have been documented. These include increased flowering, enhanced vegetative vigor and productivity, increased as well as decreased mortality, increased germination and recruitment (Daubenmire

1968, Glenn-Lewin et al. 1990, Vogl 1974). However, usually only one or two important life history parameters have been studied in the same species at the same time. Only rarely have the demographic consequences of fire been studied by following marked individuals (Hartnett and Richardson 1989, Paige 1992, Silva et al. 1991), and most such studies were carried on for only one or two years. However, knowing the effects of disturbances such as fire on plant demography is required to understand the mechanisms causing changes in species abundances and community composition (Hartnett and Richardson 1989).

The season in which fire occurs may affect how plant species and communities respond (Biondini et al. 1989, Abrahamson 1984, Howe 1995). In the Great Plains late-season fires retard the vigor of warm-season species, allowing cool-season species to increase, while early-season fires have the reverse effect (Howe 1995). Early and late dormant-season fires are commonly used in natural areas management (Steuter et al. 1990) and may have different effects on vegetation. The demographic effects of fire season on individual species has been little studied, and seasonal differences in fire effects are not known for grasslands of intermountain western North America.

Fire is a frequently used tool for managing grassland natural area preserves (Cole et al. 1992, Howe 1994, Loucks 1968), and may also be prescribed for managing populations of rare plants (Bowles et al. 1990, Grigore and Tramer 1996, Hessel and Spackman 1995). However, not all plant species respond favorably to fire, and fire effects on conservation priority species must be understood before fire management plans for

natural areas are implemented (Jacobson 1991). Silene spaldingii is an endangered plant endemic to intermountain grasslands of the Pacific Northwest. The largest known population of S. spaldingii occurs in northwest Montana on a preserve owned by The Nature Conservancy. Prescribed fire is one of the management options on this preserve. The purposes of my study are to determine: (1) the effect of fire on population persistence of Silene spaldingii, (2) how fire affects recruitment, survivorship and reproduction of S. spaldingii, and (3) the effects of fire season on the demography of S. spaldingii. ✓

Study site

Dancing Prairie Preserve is in the Tobacco Plains, a narrow glacial valley at 825 m, 6 km north of Eureka in northwest Montana (T37N R27W S26). At Fortine, ca. 27 km south and 75 m higher, mean annual precipitation was 438 mm for 1950-80. Mean July maximum and January minimum were 27.9° and -11.4°C respectively. Climate on the preserve is undoubtedly warmer and drier. The preserve currently consists of ca. 600 acres of fescue-wheatgrass-needlegrass grasslands developed on rolling glacial topography. Grasslands of western Montana are transitional between Palouse Prairie typical of eastern Washington and Oregon and grasslands of the Northern Great Plains (Antos et al. 1983). Silene spaldingii occurs in the bottom of shallow swales and on cool slope exposures with relatively deep soil. Common grasses in these habitats are Festuca scabrella, F. idahoensis and Poa pratensis (Lesica, submitted). Of these, F. scabrella is the most sensitive to fire (Mueggler and Stewart 1/2

1980). Antennaria microphylla, Arnica sorroria and Hieracium cynoglossoides were common forbs.

Fire undoubtedly played an important role in structuring the vegetation of the Tobacco Plains. Fires were ignited by Native Americans as well as by lightening (Barrett and Arno 1982) and probably played an important role in preventing the establishment of woody vegetation (Dorey 1979, Koterba and Habeck 1971). Mean presettlement fire-return interval for western Montana valleys was ca. nine years (Barrett and Arno 1982), and was estimated to be 6.4 years (range of 2-13 years) for the north end of the Tobacco Valley in southeast British Columbia (Dorey 1979).

Species description

Silene spaldingii Wats. (Caryophyllaceae) is a perennial, geophytic herb, 20-40 cm tall, from a simple or branched caudex surmounting a long, slender corm. Rhizomes or other means of vegetative propagation are lacking (Hitchcock and Maguire 1947; Lesica, pers. obs.). Flowers, borne in a branched, terminal inflorescence, bloom in July and set seed in August. Seeds will germinate with as little as four weeks of cold treatment (Lesica 1993), so germination likely occurs in fall as well as spring. Rosettes are formed the first year, after which vegetative stems are produced. New recruits may appear as vegetative stems in their first summer if they germinated the previous fall (Lesica observation). Existing plants send up new vegetation in mid-May and become senescent by early September (Lesica, submitted). Plants may become reproductive in their second season, but most

plants flower for the first time when two years or older (Lesica, submitted).

Silene spaldingii plants may go undetected for one to several years but reappear in subsequent years (Lesica, submitted; Lesica and Steele 1994). At Dancing Prairie ca. 10% of summer dormant plants produce small leaves that senesce and disappear by early July, while the remainder produce no above-ground vegetation during the entire growing season (Lesica, submitted). Prolonged dormancy can be inferred by following the fate of marked or mapped individuals for numerous years. The presence of summer dormant plants makes exact estimation of many demographic parameters difficult. At Dancing Prairie a mean of 41% of S. spaldingii plants exhibited prolonged dormancy each year in 1989-94. Of the 193 episodes of prolonged dormancy recorded during this period, 75% were one year in duration, and 90% were either one or two years long (Lesica, submitted). Thus, ca. 41% of S. spaldingii plants could not be detected in the first and last years of the study (1991, 1996); ca. 10% of plants could not be detected in the second and second to last years (1992, 1995); and only ca. 4% ($10\% \times 41\%$) of plants were undetected in 1993-94 (Lesica, submitted).

Silene spaldingii is endemic to the Palouse region of southeast Washington and adjacent Oregon and Idaho and is disjunct in northwest Montana (Hitchcock and Maguire 1947). Much of the habitat of S. spaldingii has been lost to agricultural development. Although once widespread in the Palouse region, S. spaldingii is now known from mainly isolated sites on the periphery of its former range. Most remaining populations are

small and threatened by exotic weed encroachment, livestock grazing, and herbicide treatment. Silene spaldingii is listed as threatened or endangered in all four states in which it occurs (Lesica and Shelly 1991) and is currently being considered for listing under the Federal Endangered Species Act.

Methods

Field methods

In July 1991 I established 30 113-m² (6 m radius) circular plots in the north end of the preserve where S. spaldingii plants are most common. Plot centers were permanently marked by driving a metal rod into the ground and affixing a tag with the plot number. I located plots so that each would contain at least ten plants of S. spaldingii; otherwise plot location was essentially random. In each plot I recorded the location of each plant of S. spaldingii by measuring the distance from the center post to the nearest 1-cm and the compass bearing from the plant to the post to the nearest degree. For each annual census I recorded the growth form, reproductive status, and fecundity of each S. spaldingii plant using the following classification:

Rosette, lacking any visible stem elongation

Dormant- no above-ground parts observed

Vegetative- one or more stems present but no flowers

Reproductive- one or more fertile stems present. The number of flowers was recorded for each reproductive plant.

I employed a stratified-random design to assign the plots to the three treatments: fall burn, spring burn and control. I ordered the plots according to the number of S. spaldingii plants

they contained and then divided the 30 plots into ten consecutive groups of three. One plot from each group was assigned to each of the three treatments using a random numbers table.

I divided each plot into four equal cells along the four principal compass bearings for the purpose of mapping and censusing. When several S. spaldingii plants occurred in close proximity, making individual identification uncertain, I eliminated the cell in which they occurred from analysis of that plot for all years. I eliminated 11 such cells: five fall burn, four spring burn, and two control.

The fall burn treatment was carried out mid-September 1991, and the spring burn was performed in mid-April 1992. These are the two times of year when prescribed fire is feasible on the preserve. A border approximately 3 ft wide was mowed around each plot, and the debris was raked clear. Fires were started with a drip torch and extinguished after the entire plot had been burned.

Annual censusing of Silene spaldingii plants was conducted in mid-July 1991-1996, when the plants were flowering. At the same time in 1992 I also recorded observations on the intensity of burns in the treatment plots based on the amount of litter remaining. I used these observations to place burns into one of two intensity classes: high and medium. A high intensity burn left little litter; mineral soil was apparent throughout most of the plot. In a medium intensity burn thin layers of fine litter and ash were apparent over at least half of the plot. There were no low intensity burns with coarse fuels remaining in any of the treatment plots. In 1996 I measured the depth of plant litter to

intensity
inferred
from
vegetation

the nearest 1 cm at four points, 3 m from plot center along primary compass bearings, in each plot.

Data analysis

Repeated measures analysis was used to test hypotheses regarding recruitment, survivorship, proportion of reproductive plants, flowering, proportion of dormant plants, and total density of Silene spaldingii. Each analysis for multi-year post-burn treatment effect was followed by contrast tests for a difference between burn and control treatments and between the two burn treatments. For each demographic parameter I performed one-way analysis of variance (ANOVA) for separate years in order to determine in which years the effect was present. Count and proportion variables were square-root and arcsine transformed respectively to conform to the assumptions of the tests (Sokal and Rohlf 1981, p. 421-28). Plot means for flowers per reproductive plant were not transformed prior to analysis. The 1991 preburn recorded plot densities, unbiased with respect to treatment, were used as covariates in analysis of recruitment, survivorship and total plant density to adjust for pretreatment differences among plots. The 1991 plot means were used as a covariate in the analysis of flowering. A probability level of $P=0.05$ was used to assign statistical significance. Significance levels were not adjusted for multiple tests (Stewart-Oaten 1995). Untransformed plot means for litter depth were analyzed with ANOVA.

With rare exceptions, all rosette S. spaldingii plants are new recruits. Plants in the vegetative size class may be new

recruits as well, but they may also be older (Lesica, submitted). For example, a vegetative-size plant first appearing in 1993 may be a new recruit but it could also be an older plant that was dormant in 1991-92. After 1993 ca. 96% of all plants recorded for the first time are new recruits. Only rosette plants were counted as recruits in 1991-93, while all vegetative plants recorded for the first time were also considered recruits in 1994-96.

Annual estimates of total plant density and proportion of dormant S. spaldingii plants were confounded by the inability to detect all plants in all years (see above). By eliminating the initial and final two years of data, acceptable levels of accuracy were achieved; 1993-94 estimates were ca. 96% accurate. The proportion of summer dormant plants was measured as the number of dormant plants divided by the total number of plants minus the number of recruits.

Only plants that failed to reappear for at least three consecutive years were assumed dead (see above). Survival of S. spaldingii plants observed in 1991 was analyzed for 1992-94. Survival of cohorts recruited in 1992 and 1993 was analyzed through 1994. Survivorship of combined plot totals for the 1991 sample population and the two cohorts was also analyzed using the non-parametric logrank test (Pyke and Thompson 1986; Hutchings et al. 1991).

Results

Burn intensity and litter

Burn intensity appeared to be higher in fall burn compared to spring burn plots. For the fall burn treatment, fire intensity was rated high in all but one of the plots, while it was medium intensity in all but one of the spring burn plots. The lower intensity burn in the spring is likely the result of the generally moister conditions present at that time of year compared to autumn.

Mean depth of litter in 1996 was 8.7, 9.6 and 11.1 cm in fall and spring burn plots and control plots respectively, and differences between treatments and control ($F_{1,27}=1.9$, $P=0.18$) and between fall and spring burn treatments ($F_{1,27}=0.3$, $P=0.56$) were not significant. Although the depth of litter in burn plots was similar to control levels in 1996, it appeared to me that density of fine litter was higher in control plots.

Recruitment

Recruitment of Silene spaldingii was sporadic. No recruitment (i.e., rosette plants) was detected in treatment or control plots in 1991, the year preceding the burn treatment. Recruitment was high only in 1993 in control plots, while in burn plots it was high in both 1992 and 1993 (Fig. 1A). During 1992-96 mean number of recruits per plot averaged 6.1, 5.7, and 3.2 for fall and spring burns and control respectively, significantly higher in burn plots compared to controls ($F_{5,130}=5.3$, $P<0.001$). Burn plots averaged 5.1, 1.7, and 2.0 times more recruits than controls in 1992, 1993 and 1994 respectively; differences were

significant in 1992 and 1994 and marginally significant ($P=0.08$) in 1993 (Fig. 1A). There were no differences between treatment and control plots in 1995 and 1996, the final two years of the study.

Plots burned in spring had higher recruitment than fall burn plots in 1992-96 ($F_{5,130}=4.3$, $P=0.001$). Spring burn plots had higher recruitment in 1992, while recruitment was higher in fall plots in 1993, although this difference was only marginally significant ($P=0.09$). There were no differences in recruitment between the two treatments thereafter (Fig. 1A).

Survivorship

Survivorship could be accurately estimated only through 1994. Survivorship of adult plants was high with ca. 80% survival between 1991 and 1994. There was no difference in survival of the *S. spaldingii* plants recorded in 1991 between burn plots and controls in 1992-94 ($F_{3,78}=0.7$, $P=0.49$; logrank test $\chi^2=0.31$, $P=0.58$; Fig. 2A). Survivorship of new recruits was appreciably lower than for adults, with nearly 50% mortality in the first two years. There appeared to be a tendency for greater two-year survival of the cohort recruited in 1992 in control plots (Fig. 2A); however, this difference was not significant ($F_{2,52}=0.56$, $P=0.58$; $\chi^2=0.22$, $P=0.64$), possibly due to the small number of control recruits. There was no difference in one-year survival of the 1993 cohort between treatment and control plots ($F_{1,26}=0.1$, $P=0.74$).

There were no differences in survivorship between spring and fall burn treatments for the 1991 sample population ($P=0.70$), 1992 cohort ($P=0.19$), or 1993 cohort ($P=0.60$).

Prolonged dormancy

I could accurately estimate the proportion of summer dormant S. spaldingii plants per plot only in 1993 and 1994. The proportion of dormant plants varied widely between these two years; 13-30% in 1993 and 46-79% in 1994. Control plots had more dormant plants than burn plots in 1993-94 ($F_{2,54}=15.9$, $P<0.001$). However, there were significantly more dormant plants in burn plots in 1993 ($F_{1,26}=7.7$, $P=0.01$), but significantly more in control plots in 1994 ($F_{1,26}=13.8$, $P=0.001$; Fig. 1B).

There were no differences in summer dormancy between spring and fall burns over these two years ($P=0.55$).

Reproduction

The mean proportion of recorded S. spaldingii plants in reproductive condition varied between 0.45-0.52 in 1992 to 0.79-0.82 in 1995 (Fig. 1C). Mean proportions for fall burn, spring burn, and control for 1992-96 were 0.59, 0.64 and 0.63 respectively. The mean proportion of reproductive plants in treatment and control plots were nearly equal in 1991, before the burns ($F_{1,27}=0.1$, $P=0.77$), but there were more reproductive plants in control plots in 1992-96, although the difference was only marginally significant ($F_{5,130}=2.2$, $P=0.055$). The difference was primarily due to a 20% higher proportion of reproductive plants in control plots in 1993 ($F_{1,26}=4.25$, $P=0.049$; Fig 1.). Treatment

and controls were not different in any other year following the burn ($P>0.47$, Fig. 1C).

The mean proportion of reproductive plants was not significantly different between fall and spring burn treatments in 1991 ($F_{1,27}=1.3$, $P=0.26$) or in 1992-96 ($F_{5,130}=0.5$, $P=0.76$).

The mean number of flowers per reproductive S. spaldingii plant per plot in 1991 was 5.4, 4.9 and 5.8 for fall burn, spring burn and control respectively, and difference between treatments and control was not significant ($F_{1,27}=1.27$, $P=0.27$). Following the burn in 1992-96, burn plots had significantly more flowers per plant than controls ($F_{5,115}=3.63$, $P=0.004$); mean number of flowers per plant per plot was 6.2, 6.2, and 5.7 for fall burn, spring burn and control respectively. The trend for greater flowering in burn plots was marginally significant in 1992 and 1993 ($P=0.09$) and was no longer apparent after 1994 (Fig. 1E).

There was no difference in flowering between fall and spring burns in 1992-96 ($P=0.76$).

Population trends

Accurate estimates of mean total number of S. spaldingii plants per plot could be obtained only for 1993 and 1994. There was no difference between treatment and control plots in mean number of plants detected in 1991 ($F_{1,27}=0.2$, $P=0.66$), and because the plots were assigned randomly, I assume that there were no important differences in total number of plants either. In both treatment and control plots there were more plants in 1993 than 1994 (Fig. 1D). In 1993-94 mean number of plants was 55.5, 56.2, and 45.9 in fall and spring burn and control plots respectively

and the difference between treatments and control was significant ($F_{2,52}=3.9$, $P=0.025$) when among plot differences in 1991 were controlled for. Although total number of S. spaldingii plants in burn plots tended to be greater in both years, the difference was significant only in 1994 ($F_{1,26}=5.9$, $P=0.02$; Fig. 1D).

There was no difference in the plant density between fall and spring burn plots in 1993-94 ($P=0.98$).

Discussion

Effects of fire

Enhanced recruitment and a concomitant increase in population size were the principal effects of fire on Silene spaldingii in this study. The number of recruits averaged more than twice that of controls over the three years following fire. In the fourth and fifth years following fire, recruitment of S. spaldingii in treatment plots was no longer higher, and litter accumulations in treatment plots was approaching that of controls. Seeds and newly emerged seedlings of S. spaldingii are small, and survival of seedlings beneath the deep layer of bunchgrass litter is likely to be low. The negative correlation between the canopy cover of F. scabrella and the density of S. spaldingii in these habitats (Lesica, submitted) supports this hypothesis. Interspecific interference through litter accumulation has been demonstrated in other species (Bergelson 1990) and is thought to be the cause of reduced diversity in some grassland systems (Tilman 1993; see reviews in Facelli and Pickett 1991, Vogl 1974). Reduction of the litter layer by grazing or fire is expected to result in increased small seedling

survival and is the most likely cause of the higher rates of recruitment observed in burn plots in this study. Grassland fires may also result in warmer soil temperatures and increased available nutrients (Hulbert 1988, Knapp and Seastedt 1986, Raison 1977) which could cause enhanced germination and recruitment (Daubenmire 1968, Glenn-Lewin et al. 1990).

The effect of fire on the reproductive capacity of S. spaldingii was equivocal. Over the period of 1992-96, the proportion of reproductive plants in spring burn and control plots was nearly equal, but was lower following the fall burn treatment. The number of flowers per reproductive plant was greater in burn plots, but this trend was apparent for only 2-3 years following the treatments. It is not known whether the increase in flowering translated into an increase in seed production. These effects of fire on reproductive capacity did not likely have an effect on recruitment in 1992-93. However, increased seed set that may have resulted might affect recruitment in the future, depending on seed bank dynamics, disturbance regime, and weather. Increased flowering and seed production has often, but not always been reported for grassland species following fire (Daubenmire 1968, Vogl 1974). Silene regia, a congener of eastern North American grasslands, responds to fire with increased density of reproductive stems and number of flowers per stem (Menges 1995).

Fire had no detectable effect on the survival of adults or recruits of Silene spaldingii. Some studies in grassland systems have found that fire can increase size and survival of grasses and forbs (Hartnett and Richardson 1989, Silva et al. 1991),

while others have found that survivorship decreased (Paige 1992). The effect of fire on a species often depends on the season in which the burn occurs (Howe 1995), and this may explain some of the variation in results reported in the literature. In my study, neither burn treatment had a significant effect on survivorship, probably because they occurred before and after the plant's active growing season. In northwest Montana, lightning-caused fires would have occurred most frequently during July and August (**reference**). Fire at this season would likely have a more adverse effect on S. spaldingii because plants are actively growing and flowering at that time.

I was able to pinpoint the significant effects of fire on the demography of Silene spaldingii by following the fate of individual plants for five summers following burn treatments. Studies in which plots are simply censused following treatments may not be able to distinguish between changes in survival and recruitment. Furthermore, studies documenting enhanced recruitment following fire without determining recruit survivorship may not accurately predict the ultimate effect of the treatment if survival is low. Herbaceous geophytes that demonstrate prolonged dormancy present a particularly vexing problem when studying the effects of fire. Changes in the density of detectable plants may or may not indicate real changes in population size, especially since fire may affect the proportion of summer dormant plants in complex ways. Few studies have taken advantage of demographic methods to study fire effects on herbaceous plants. Silva et al. (1991) followed individual plants in experimental burns and controls and used matrix

projection models to show that survival, growth and reproduction of smaller plants were important rates in a perennial savannah grass. They found that fire enhanced these vital rates, allowing this grass to persist in fire-managed systems. Clearly, employing demographic methods in experimental designs has many advantages.

Effects of fire season

Season of fire can be important to the effects of burn treatments on herbaceous plants (Howe 1995), and my study demonstrated a between-fire season effect on recruitment in S. spaldingii. A greater amount of residual fine litter in spring compared to fall burn plots indicated higher intensity fire for the fall burn, probably due to lower fuel moisture at that time of year. Fall burn plots had lower Silene spaldingii recruitment in 1992, resulting in lower recruitment for the entire study period. The thin layer of fine litter remaining after the cooler spring burn may have provided better safe sites for germination and survival. Whatever the cause, differences between the two treatments did not ultimately translate into a significant difference in mean density of S. spaldingii.

Prolonged dormancy

The proportion of summer dormant plants was lower for burn (0.38) compared to control (0.46) plots in 1993-94. However, the number of dormant plants was higher for burn plots in 1993 but higher in controls in 1994 (Fig. 1B). In addition the between-year variation in prolonged dormancy was smaller in burn plots

compared to controls. At Dancing Prairie Preserve prolonged dormancy of S. spaldingii demonstrated biennial cycles in 1989-94 with a higher proportion of dormant plants occurring in even-numbered years (Lesica, submitted). It appears that fire had a damping effect on this cycle, raising the low proportion of dormant plants in 1993 and raising the proportion in 1994.

Understanding the mechanism responsible for fire-induced change in rates of prolonged dormancy is problematic because the causes of prolonged dormancy are not understood. Environmental stresses such as drought or flooding have been invoked to explain high levels of prolonged dormancy (Lesica and Steele 1994), but evidence is generally anecdotal. Winter temperature and amount of summer precipitation were positively correlated with the proportion of summer dormant S. spaldingii plants the following year at Dancing Prairie in 1989-94 (Lesica, submitted). However, it is difficult to imagine a mechanism to explain these correlations. The biennial cycling of prolonged dormancy of S. spaldingii plants suggests that an endogenous, physiological rhythm synchronized by an environmental cue could play a role (Lesica, submitted). A high rate of summer dormancy for the flush of 1992 recruits in burn plots might partly account for higher treatment dormancy in 1993; however, the proportion of plants dormant in 1993 was nearly equal for 1992 recruits (38%) and non-recruits (36%; $\chi^2=0.28$, $P=0.60$). Perhaps the warmer early spring ground temperatures or enhanced nutrient availability following fire induce a significant proportion of plants to shift their cycles by one year.

Management considerations

Disturbances such as fire or grazing that reduce the quantity of litter in highly productive grasslands are likely to be important to the long-term persistence of Silene spaldingii. Grazing by large ungulates is thought to have been of minor importance in the evolution of grassland ecosystems in most of intermountain western North America (Mack and Thompson 1982), although wapiti (Cervus canadensis) may have had some impact in northwest Montana. On the other hand, fire was a common occurrence in these intermountain grasslands (Barrett and Arno 1982) and undoubtedly played a role in shaping presettlement plant communities (Koterba and Habeck 1971). Fire is a preferred management tool at Dancing Prairie Preserve for ecological and logistical reasons (B. Martin, The Nature Conservancy; pers. comm). In the absence of fire and grazing, significant recruitment of S. spaldingii is episodic (Lesica, submitted). My study has shown that fire can enhance recruitment and population density of S. spaldingii at Dancing Prairie Preserve. In the absence of grazing, fire may be required to reduce litter and allow adequate recruitment of S. spaldingii and other ecologically similar species. In eastern Washington S. spaldingii occurs in less productive grasslands in which substantial accumulations of litter do not occur. Fire may not demonstrate positive effects on S. spaldingii at these sites. ← citation?

My study suggest that burning productive grasslands will have a positive effect on S. spaldingii whether prescribed in spring or fall. With regard to conservation of S. spaldingii, there is little reason to chose fall rather than spring burning

one, although recruitment may be somewhat higher following a spring burn.

Enhanced recruitment of S. spaldingii persisted for three years following burn treatments. Depth of litter accumulation in burn plots reached control levels five years after the treatments, although litter density still appeared higher in controls after this length of time. Presettlement fire return intervals were ca. 6-9 years (Barrett and Arno 1982, Dorey 1979). These results suggest that a fire intervals of ca. 5-10 years would be appropriate for the preserve and provide optimum growth rates of S. spaldingii populations in these habitats. Shorter intervals may not allow accumulation of sufficient fuel loads to carry a fire, and there would be little benefit to recruitment rates.

Acknowledgements

Bernie Hall, Karen Bray and Linda and Louis Young conducted the burn treatments. Brian Steele provided advice on statistical procedures. Funding was provided by a Katherine Ordway Stewardship Foundation grant, the USDA Forest Service Intermountain Research Station, and the Montana Office of The Nature Conservancy.

Literature Cited

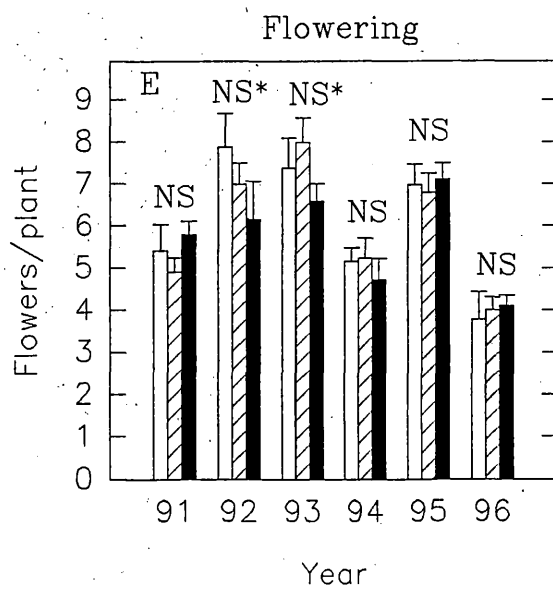
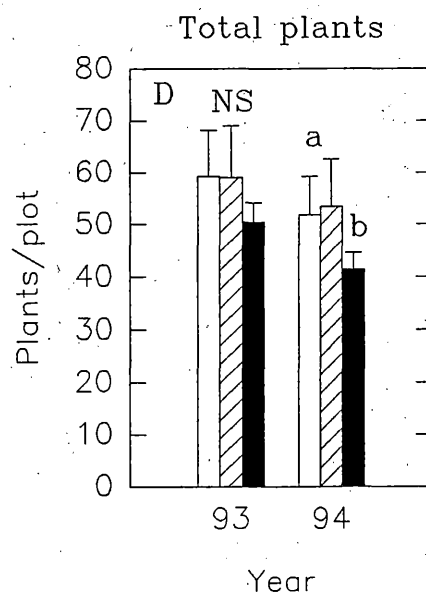
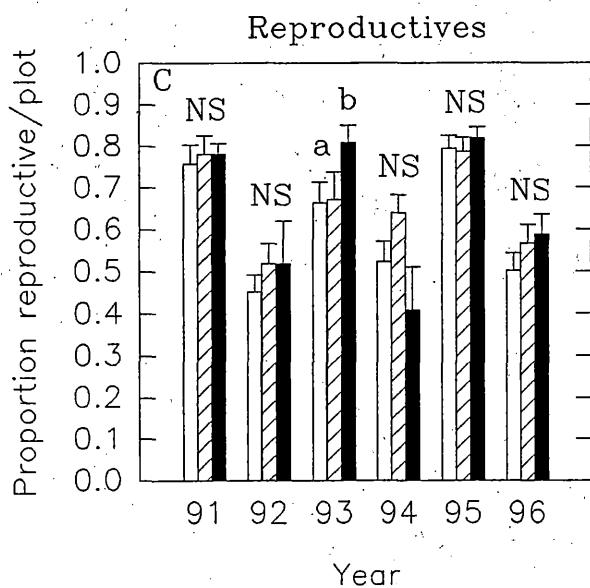
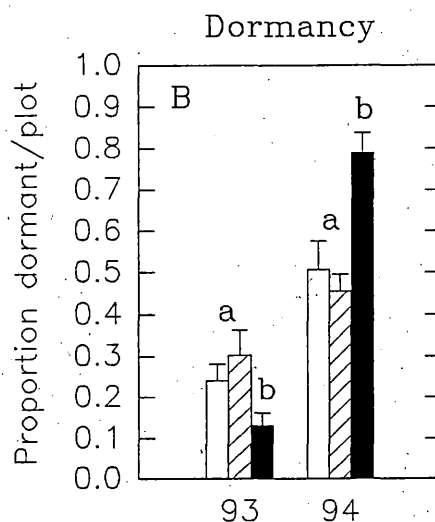
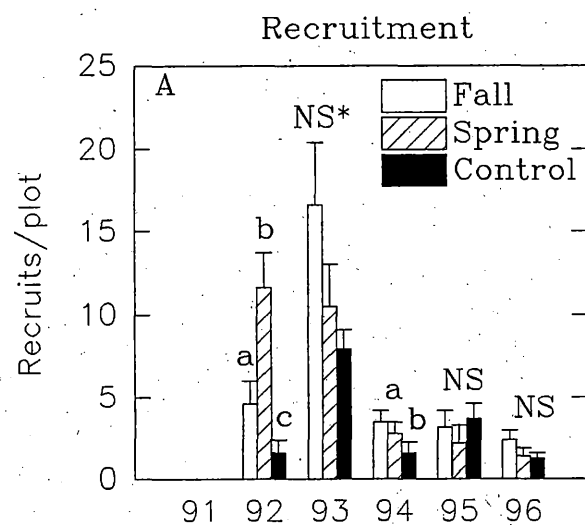
- Abrahamson, W. G. 1984. Species responses to fire on the Florida Lake Wales Ridge. *American Journal of Botany* 71: 35-43.
- Antos, J. A., B. McCune and C. Bara. 1983. The effect of fire on an ungrazed western Montana grassland. *American Midland Naturalist* 110:354-364.
- Barrett, S. W. and S. F. Arno. 1982. Indian fires as a n ecological influence in the Northern Rockies. *Journal of Forestry* 80: 647-651.
- Bergelson, J. 1990. Life after death: site preemption by the remains of Poa annua. *Ecology* 71: 2157-2165.
- Biondini, M. E., A. A. Steuter, and C. E. Grygiel. 1989. Seasonal fire effects on the diversity patterns, spatial distribution, and community structure of forbs in the Northern Mixed Prairie. *Vegetatio* 85: 21-31.
- Bowles, M. L., M. M. DeMauro, N. Pavlovic and R. D. Hiebert. 1990. Effects of anthropogenic disturbances on endangered and threatened plants at the Indiana Dunes National Lakeshore. *Natural Areas Journal* 10: 187-200.
- Brewer, J. S. 1995. The relationship between soil fertility and fire-stimulated floral induction in two populations of grass-leaved golden aster, Pityopsis graminifolia. *Oikos* 74: 45-54.
- Cole, K. L., K. F. Klick, and N. B. Pavlovic. 1992. Fire temperature monitoring during experimental burns at Indiana Dunes National Lakeshore. *Natural Areas Journal* 12: 177-183.
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.
- Daubenmire, R. 1968. Ecology of fire in grasslands. *Advances in Ecological Research* 5: 209-266.
- Dorey, R. J. 1979. A fire history investigation and the effects of fire exclusion on a ponderosa pine forest in southeastern British Columbia. B.S. Thesis, University of British Columbia, Vancouver.
- Dudley, J. L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130: 286-298.
- Facelli, J. M. and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57: 1-32.
- Glenn-Lewin, D. C., L. A. Johnson, T. W. Jurik, A. Kosek, M. Leoscheke, and T. Rosburg. 1990. Fire in central North American grasslands: vegetative reproduction, seed germination and seedling establishment. Pages 28-45 in S. L. Collins and L. L. Wallace (eds.), *Fire in central North American grasslands*. University of Oklahoma Press, Norman.
- Grigore, M. T. and E. J. Tramer. 1996. The short-term effects of fire on Lupinus perennis L. *Natural Areas Journal* 16: 41-48.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107-145.

- Hartnett, D. C. and D. R. Richardson. 1989. Population biology of Bonamia grandiflora (Convolvulaceae): effects of fire on plant and seed dynamics. *American Journal of Botany* 76: 361-369.
- Hessl, A. and S. Spackman. 1995. Effects of fire on threatened and endangered plants: an annotated bibliography. USDI National Biological Service Information and Technology Report 2, Washington D.C.
- Hitchcock, C. L. and B. Maguire. 1947. A revision of the North American species of Silene. University of Washington Publications in Biology 13: 1-73.
- Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology* 8: 691-704.
- Howe, H. F. 1995. Succession and fire season in experimental prairie plantings. *Ecology* 76: 1917-1925.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* 50: 874-877.
- Hulbert, L. C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* 69: 46-58.
- Huston, M. A. 1994. Biological diversity. Cambridge University Press, Cambridge.
- Hutchings, M. J., K. D. Booth, and S. Waite. 1991. Comparison of survivorship by the logrank test: criticisms and alternatives. *Ecology* 72: 2290-2293.
- Jacobson, G. L. 1991. Conservation of rare plant habitat: insights from the recent history of vegetation and fire at Crystal fen, northern Maine, USA. *Biological Conservation* 57: 287-314.
- Knapp, A. K. and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36: 662-668.
- Koterba, W. D. and J. R. Habeck. 1971. Grasslands of the North Fork Valley, Glacier National park, Montana. *Canadian Journal of Botany* 49: 1627-1636.
- Kozlowski, T. T. and C. E. Ahlgren (eds.). 1974. Fire and ecosystems. Academic Press, New York.
- Lesica, P. 1993. Loss of fitness resulting from pollinator exclusion in Silene spaldingii (Caryophyllaceae). *Madrono* 40: 193-201.
- Lesica, P. Submitted. Demography of the endangered plant, Silene spaldingii (Caryophyllaceae) in northwest Montana. *Madrono*.
- Lesica, P. and J. S. Shelly. 1991. Sensitive, threatened and endangered vascular plants of Montana. Montana Natural Heritage Program, Occasional Publication No. 1. Helena, MT.
- Lesica, P. and B. M. Steele. 1994. Prolonged dormancy in vascular plants and implications for monitoring studies. *Natural Areas Journal* 14: 209-212.
- Loucks, O. L. 1968. Scientific areas in Wisconsin. Fifteen years in review. *BioScience* 18: 396-398.
- Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119: 757-773.

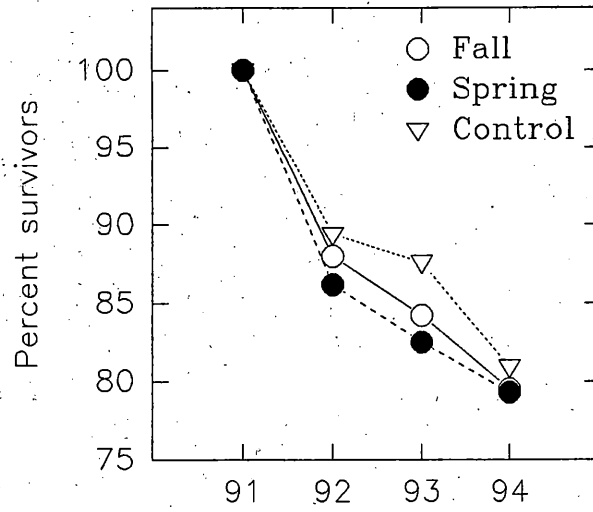
- Menges, E. S. 1995. Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated prairie forb. *American Midland Naturalist* 133: 242-255.
- Mueggler, W. F. and W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA General Technical Report INT-66, Ogden, UT.
- Paige, K. N. 1992. The effects of fire on scarlet gilia: an alternative selection pressure to herbivory? *Oecologia* 92: 229-235.
- Peet, M. R., R. Anderson and M. S. Adams. 1974. Effect of fire on big bluestem production. *American Midland Naturalist* 94: 15-26.
- Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. *Bulletin of Torrey Botanical Club* 107: 238-248.
- Pickett, S. T. A. and P. S. White (eds.). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL.
- Pyke, D. A., and J. N. Thompson. 1986. Statistical analysis of survival and removal experiments. *Ecology* 67: 240-245.
- Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformation: a review. *Plant and Soil* 51: 73-108.
- Silva, J. F., J. Raventos, H. Caswell and M. C. Trevisan. 1991. Population responses to fire in a tropical savannah grass, *Andropogon semiberbis*: a matrix model approach. *Journal of Ecology* 79: 345-356.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, San Francisco.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.
- Steuter, A. A., C. E. Grygiel and M. E. Biondini. 1990. A synthesis approach to research and management planning: the conceptual development and implementation. *Natural Areas Journal* 10: 61-68.
- Stewart-Oaten, A. 1995. Rules and judgements in statistics: three examples. *Ecology*, 76: 2001-2009.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.
- Vogl, R. J. 1974. Effect of fire on grasslands. Pages 139-194 in T. T. Kozlowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York.
- Watt, A. S. 1981. A comparison of grazed and ungrazed grassland A in East Anglian Breckland. *Journal of Ecology* 69: 499-508.

Figure 1. Mean (A) number of recruits, (B) proportion of dormant plants, (C) proportion of reproductive plants, (D) total number of plants, and (E) number of flowers per plant for Silene spaldingii in fall and spring burn and control plots in 1991-96. In each year, different letters indicate significant differences between treatments ($P < 0.05$) by ANOVA. * indicates marginal significance ($0.05 < P < 0.10$).

Figure 2. (A) Depletion curves for 1991 sample population and (B) survivorship curves for 1992 cohort of Silene spaldingii for fall and spring burn treatments and control.



1991 Sample population



1992 cohort

